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# VASCULAR EPIPHYTES: THEIR SYSTEMATIC OCCURRENCE AND SALIENT FEATURES

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One of the characteristic features of wet tropical vegetation is the abundance of epiphytes covering the limbs and trunks of the forest trees and hanging in masses from the outer branches. These plants have intrigued botanists since the early days of tropical exploration, yet they remain poorly known both taxonomically and biologically. While numerous book-length reviews have appeared in the last decade on such plant associations as mangroves, bog plants, strand plants, and vascular aquatics, there has been no equivalent general review of epiphytes since that of Schimper in 1888. It was hoped that with the founding in 1973 of the Marie Selby Botanical Gardens, an institution specializing in the study of epiphytes, that this situation would be remedied. The intent of the present paper is to delimit and describe the vascular epiphytes in terms of their systematic composition and their major features.

## Materials and Methods

A preliminary list of genera of vascular epiphytes was compiled from the literature and my own collections. This list was circulated for corrections and additions to the following persons: C. H. Dodson, R. L. Dressler, R. A. Howard, J. Luteyn, T. Plowman, L. B. Smith, P. F. Stevens, J. Steyermark, B. C. Stone, P. van Royen, H. Wiehler, and J. Wurdack. Collectively these individuals have a formidable first-hand knowledge of the world's tropical floras, and their assistance is gratefully acknowledged.

Specimens of all the genera on the emmended list were examined at the Harvard University Herbaria (A and GH) to ascertain the approximate numbers of epiphytic species per genus and to note the occurrence of certain features such as adventitious roots and type of fruits and seeds. Extensive use was made as well of floras and monographs in compiling this information. In a few cases I have omitted citation of genera suggested by the above correspondents where all of a large number of herbarium specimens were non-epiphytes.

The final list (Table 1) is in four categories — pteridophytes, gymnosperms, monocotyledons, and dicotyledons, and within each category the families are listed alphabetically. Following the name of each family and genus are two numbers separated by a / : the first of these is the number of epiphytic species in the taxon and the second the total number of species in the taxon. In some cases estimation of the number of epiphytic species is very approximate. The figure for the total number of species per taxon is that given by Willis (1973), except where corrected for differences in generic delimitation (e.g. ferns and Cactaceae). The geographic region in which the epiphytic species of a genus are found is indicated; this may be considerably less than the range of the genus as a whole. The fruit or seed type in each genus is indicated by one of three letters: 'D' for dust-seed, (minute, unappendaged, wind-dispersed seeds), 'W' for winged or plumed seeds of capsular fruits, and 'F' for fleshy fruits whether berries, drupes, or fleshy capsules with animal-dispersed seeds.

In the ferns I follow the generic and familial treatment of Copeland (1947) except for the Hymenophyllaceae in which I recognize only the two large genera *Hymenophyllum* and *Trichomanes*. The Cactaceae are cited

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according to the generic concepts of Britton & Rose (1937). In other families where generic limits are uncertain, e.g. Ericaceae, Rubiaceae, my treatment for the most part reflects the arrangements followed in the Harvard University Herbaria. For the Orchidaceae, which has by far the greatest number of genera and species of epiphytes of any family, I have not attempted to list the genera but only estimated the total number of genera and species. The list of genera of epiphytes presented in Table 1 is very likely still incomplete, though it probably includes all of the major epiphytic genera. The reader is invited to send additions, corrections, and comments to the author.

I have not undertaken a review of the literature on epiphytes at this time, and there are a number of unsupported assertions in the text. Nearly all of these are based at least in part on examination of herbarium specimens and/or living plants in the wild or in cultivation. In this I have been fortunate in having at hand the large collection of living epiphytes of the Marie Selby Botanical Gardens. An annotated bibliography on vascular epiphytes is being prepared for publication in a later issue of SELBYANA.

## DEFINITION OF 'EPIPHYTE'

As with many ecologically determined categories, 'epiphyte' shades off into other growth forms in several directions. As 'true epiphytes' may be considered those species which normally germinate on the surface of another living plant and pass the entire life cycle without becoming connected to the ground. However in compiling this list I have taken a broader view of the term 'epiphyte' to include all plants which at some stage in their life cycle are normally not connected to the ground by a stem. They may be connected by roots, as in some Araceae with terrestrial germination which become epiphytic later in life by rotting away of the early stem, though retaining terrestrial contact by long adventitious roots. Also included are species which germinate in the trees and are initially epiphytic, but later become connected to the ground by roots, and may even eventually become free-standing trees (e.g. *Ficus, Clusia, Griselinia*).

In addition to species in which all of the individuals are epiphytic for part of the life cycle there are a number of species where a portion of the population consists of true epiphytes and the remaining individuals are terrestrial. This is especially common in Ericaceae and Myrtaceae where growth habit is plastic and a single species may occur as a lithophyte, epiphyte, liana, or tree depending on where it happens to germinate. I have generally included such species in the list while at the same time trying to exclude accidental epiphytes. A great many species with no adaptations to epiphytic life may be found occasionally growing in a pocket of soil in the persistent leaf bases of a palm or on a rotting stump. Ridley (1930) lists a sizeable flora of accidental epiphytes on pollard willows in Europe. These species are not included in the present list.

Also excluded from Table 1 are the parasitic epiphytes, plants with a direct vascular connection to their host. These represent a highly specialized group systematically and physiologically distinct from non-parasitic epiphytes. Parasitic epiphytes apparently evolved from root-parasite ancestors (Kuijt 1969).

## SYSTEMATIC OCCURENCE OF VASCULAR EPIPHYTES

Epiphytes are found in 65 families of vascular plants (Table 1). Of these, 9 families are pteridophytes with a total of 89 genera and 2510 species of epiphytes. The gymnosperms are represented by only two families with two genera and four species, the monocotyledons (excepting orchids) by 15

families with 63 genera and 1850 species, and the dicotyledons by 38 families with 198 genera and 3800 species of epiphytes. The total (less Orchidaceae) is 352 genera and about 8160 species of vascular epiphytes. To this must be added approximately 500 genera and 20,000 species of epiphytic Orchidaceae for a total of 850 genera and 28,200 species of vascular epiphytes. Conservatively, an additional several thousand species remain undescribed. The epiphytes must thus be considered to include at least 10% of the species of vascular plants.

The most striking aspect of this list is the overwhelming significance of the Orchidaceae in numbers; more than two thirds of the species of epiphytes are orchids. Much of the speciation in the Orchidaceae is the result of adaptive radiation in pollination ecology not directly related to epiphytism. However among the epiphytic orchids there has also been considerable diversification of growth habit and habitat preference unmatched by any other family and which accounts in part for the great number of epiphytic species.

Other major families of epiphytic monocotyledons are the Araceae and Bromeliaceae. Most of the aroids are hemi-epiphytes with terrestrial germination, but a number of true epiphytes are found in the genera *Anthurium*, *Philodendron*, *Remusatia* and *Stenospermation*. The Bromeliaceae are a highly specialized group and are perhaps the best known of the epiphytes in terms of physiology and taxonomy. They constitute the most conspicuous component of the neotropical epiphytic vegetation.

Among the dicotyledons the majority of the epiphytic species pertain to only a few families. The Asclepiadaceae, Cactaceae, Ericaceae, Gesneriaceae, Melastomataceae, Moraceae, Piperaceae, and Rubiaceae together ininclude about 90% of the total.

The systematic relationships of the epiphyte-containing families do not fit any obvious pattern in either the Engler-Prantl or Cronquist schemes of classification. It is notable, however, that all of the angiospermous epiphytes (with the possible exception of some Piperaceae) are animal-pollinated; epiphytes have not arisen in primarily anemophilous groups. A factor here may be the relative absence of steady light winds favorable for pollination in the wet tropical forest which constitute the chief habitat of epiphytes. On the other hand, the majority of epiphytes has wind-dispersed diaspores; infrequent and strong winds may be more effective in this regard.

None of the families on the list is exclusively epiphytic (except Vittariaceae) nor does it seem likely that any of them is derived from a primarily epiphytic ancestor. Rather in each case epiphytism is probably a recent adaptation within an otherwise terrestrial family. The epiphytic habit of growth may thus be considered to have arisen independently at least 65 times, and probably more. For instance, there are at least three independent origins in the Araceae and two in *Utricularia*, (personal communication from Peter Taylor).

TABLE 1. GENERA OF VASCULAR EPIPHYTES.

For each genus and family the number of epiphytic species is given, followed by the total number of species in the genus or family. For the angiosperm genera the type of seed dispersal is indicated by a D (dust seed), W (winged seed), or F (fleshy fruit). Genera in which the species are hemi-epiphytes are so indicated by the term 'hemi.'

VASCULAR EPIPHYTES

PTERIDOPHYTA

ASPIDIACEAE
*Elaphoglossum* Schott 250/400 pantropical
*Rhipidopteris* Schott 4/4 neotropics

ASPLENIACEAE
*Asplenium* L. 400/700 pantropical

DAVALLIACEAE
*Araiostegia* Copel. 12/12 India-Malaysia
*Arthropteris* J. Sm. 20/20 paleotropics
*Davallia* Sm. 40/40 Madagascar, India, Malaysia

*Davallodes* Copel. 11/11 Malaysia
*Humata* Cav. 50/50 Madagascar, India, Malaysia
*Nephrolepis* Schott 20/30 pantropical
*Oleandra* Cav. 20/40 pantropical
*Parasorus* v.A.v.R. 1/1 Moluccas
*Psammiosorus* Christensen 1/1 Madagascar
*Scyphularia* Fee 8/8 Malaysia
*Trogostolon* Copel. 2/2 Phillipines, China

HYMENOPHYLLACEAE
*Hymenophyllum* Sm. 250/300 pantropical
*Trichomanes* L. 250/300 pantropical

OPHIOGLOSSACEAE
*Ophioglossum* L. 2/50 Malaysia, neotropics

POLYPODIACEAE
*Acrosorus* Copel. 5/5 Malaysia to Somoa
*Aglaomorpha* Schott 4/4 Malaysia
*Amphoradenium* Desv. 6/6 Hawaii
*Anarthopteris* Copel. 1/1 New Zealand
*Arthromeris* (Moore) J. Sm. 69 Indomalaya
*Belvisia* Mirbel 15/15 paleotropics
*Calymmodon* Presl 25/25 Ceylon to Tahiti
*Campyloneurum* Presl 25/25 neotropics
*Christiopteris* Copel. 4/4 Malaysia & Pacific
*Cochlidium* Kaulfuss 7/7 neotropics
*Crypsinus* Presl 40/40 India, Malaysia
*Ctenopteris* Bl. 200/200 pantropical
*Dendroconche* Copel. 2/2 New Guinea
*Diblemma* J. Sm. 1/1 Phillipines
*Dictymia* J. Sm. 3/3 Australia to Fiji
*Drymotaenium* Makino 2/2 Japan, Formosa
*Drynaria* (Bory) J. Sm. 20/20 paleotropics
*Drynariopsis* (Copel.) Ching 1/1 Malaysia
*Eschatogramme* Trev. 4/4 S. Amer., W.I.
*Glyphotaenium* J. Sm. 4/4 neotropics
*Goniophlebium* (Bl.) Presl 20/20 tropical Asia-Pacific
*Grammatopteridium* v.A.v.R. 2/2 Malaysia
*Grammitis* Swartz 150/150 pantropical
*Holcosorus* Moore 2/2 Borneo
*Holostachyum* (Copeland) Ching 1/1 New Guinea
*Lecanopteris* Reinw. 15/15 New Guinea
*Lemmaphyllum* Presl 4/4 India, Malaysia
*Leptochilus* Kaul. 1/1 India, Malaysia
*Loxogramme* (Bl.) Presl 40/40 India, Malaysia
*Marginariopsis* Christensen 1/1 neotropics
*Merinthosorus* Copel. 2/2 Malaysia
*Microgramma* Presl 20/20 18 America, 2 Africa
*Microsorium* Link 40/40 paleotropics
*Nematopteris* v.A.v.R. 1/1 Borneo
*Neocheiropteris* Christ. 5/5 Indomalaya to Japan
*Niphidium* J. Sm. 2/2 Ecuador
*Oleandropsis* Copel. 1/1 New Guinea
*Oreogrammatis* Copel. 1/1 Borneo
*Paltonium* Presl 1/1 Carribean
*Paragramma* (Blume) Moore 2/2 Malaysia
*Paraleptochilus* Copel. 2/2 Indomalaya
*Pessopteris* Underw. & Maxon 1/1 neotropics
*Phlebodium* (R. Br.) J. Sm. 1/1 neotropics
*Photinopteris* J. Sm. 1/1 Malaysia
*Platycerium* Desv. 17/17 pantropical
*Pleopeltis* HBK 40/40 pantropical
*Polypodiopsis* Copel. 3/3 Borneo
*Polypodium* L. 70/75 pantropical
*Prosaptia* Presl 20/20 Indomalaya-Pacific
*Pteropsis* Desv. 6/6 Madagascar, Asia, Pacific
*Pycnoloma* Christensen 3/3 Borneo
*Pyrrosia* Mirbel 100/100 paleotropics
*Scleroglossum* v.A.v.R. 6/6 Ceylon to Pacific
*Selliguea* Bory 4/5 Malaysia-Pacific
*Solanopteris* Copel. 4/4 neotropics
*Synammia* Presl 1/1 Chile
*Thayeria* Copel. 1/1 Phillipines
*Thylacopteris* Kunze apud Mett. 1/1 Java to Luzon
*Weatherbya* Copel. 2/2 Malaysia
*Xiphopteris* Kaulfuss 50/50 pantropical

PSILOTACEAE
*Psilotum* Sw. 3/3 pantropical
*Tmesipters* Bernh. 5/7 Australia, N.Z., Pacific

SCHIZEACEAE
*Schizea* Sm. 2/30 Pacific

VITTARIACEAE
*Ananthacorus* Underw. & Maxon 1/1 neotropics
*Anetium* (Kunze) Splitg. 1/1 neotropics
*Antrophyum* Kaulf. 40/40 paleotropics
*Hecistopteris* J. Sm. 1/1 neotropics
*Monogramma* Schkurh. 2/2 Mascarenes, Malaysia
*Polytaenium* Desv. 10/10 neotropics
*Scoliosorus* Moore 1/1 C. America & Mexico
*Vaginularia* Fee 6/6 Ceylon to Fiji
*Vittaria* Sm. 80/80 pantropical

## GYMNOSPERMAE

GNETACEAE
*Gnetum* L. 3/30 Malaysia, S. Amer.

ZAMIACEAE
*Zamia* L. 1/35 C. Amer.

## MONOCOTYLEDONAE

AGAVACEAE 1/670
*Yucca* L. 1/40 Mexico F

AMARYLLIDACEAE 1/1100
*Curculigo* Gaert. 1/10 New Guinea D

APOSTASIACEAE 1/20
*Apostasia* Bl. 1/10 New Guinea D

ARACEAE 850/2000
*Amydrium* Schott 4/4 Malaysia F (hemi)
*Anthurium* Schott 400/550 neotropics F (½ hemi)
*Caladiopsis* Engl. 2/2 S. Amer. F (hemi)
*Epipremnum* Schott 15/15 Indomalaya F (hemi)
*Monstera* Adans. 24/25 neotropics F (hemi)
*Pedicellarum* Hotta 1/1 Borneo F (hemi)
*Philodendron* Schott 200/275 neotropics F (⅔ hemi)
*Porphyrospatha* Engl. 3/3 neotropics F (hemi)
*Pothos* L. 25/75 Indomalaya & Pacific F (hemi)
*Remusatia* Schott 1/4 Africa F
*Rhaphidophora* Hassk. 100/100 Indomalaya & Pacific, F (hemi)
*Rhodospatha* Poepp. 12/15 neotropics F (hemi)
*Scindapsus* Schott 20/30 Indomalaya & Pacific F (hemi)
*Stenospermation* Schott 25/25 neotropics F
*Syngonium* Schott 18/25 neotropics F (hemi)

BROMELIACEAE 919/1400
*Acanthostachys* Link, Kl. & Otto 3/3 S. Amer. F
*Aechmea* Ruiz & Pav. 120/150 S. Amer. W.I. F
*Ananas* Mill. 1/5 New Guinea (escaped from cult.) F
*Araeococcus* Brongn. 3/3 neotropics F
*Billbergia* Thunb. 45/50 neotropics F
*Brocchinia* Schult. f. 1/12 S. Amer. W
*Bromelia* L. 3/40 neotropics F
*Canistrum* Morren. 3/7 Brazil F
*Catopsis* Griseb. 20/25 neotropics W
*Glomeropitcairnia* Mez 2/2 Venezuela, W.I. W
*Guzmania* Ruiz & Pav. 75/110 neotropics W
*Hohenbergia* Bak. 2/2 S. Amer. F
*Mezobromelia* L. B. Smith 2/2 S. Amer. W
*Navia* Schult. f. 2/60 S. Amer. W
*Neoregelia* L. B. Smith 30/40 S. Amer. F
*Nidularium* Lem. 15/22 Brazil, F
*Pitcairnia* L'Herit. 15/250 neotropics W
*Portea* Brong. & C. Koch 3/6 Brazil F
*Quesnelia* Gaudich. 6/12 S. Amer. F
*Ronnbergia* E. Morr. & Andre 4/5 S. Amer. F
*Streptocalyx* Beer. 10/12 S. Amer. F
*Tillandsia* L. 400/500 neotropics W
*Vriesia* Lindl. 150/190 neotropics W
*Wittrockia* Lindm. 4/6 Brazil F

BURMANNIACEAE 2/125
*Burmannia* L. 2/57 New Guinea, S. Amer. D

COMMELINACEAE 3/500
*Campelia* Rich. 1/3 S. Amer. F
*Cochliostema* Lem. 2/2 C. & S. Amer.

COSTACEAE 4/200
*Costus* L. 4/150 Africa F

CYCLANTHACEAE 31/180
*Asplundia* Harling 20/82 C. & S. Amer. F (hemi)
*Carludovica* Ruiz & Pav. 1/3 C. Amer. F (hemi)
*Ludovia* Brongn. 2/2 S. Amer. F (hemi)
*Sphaeradenia* Harling 7/38 neotropics F (hemi)
*Thoracocarpus* Harling 1/1 S. Amer. F (hemi)

GRAMINEAE 2/10,000
*Microlaena* R. Br. 1/10 N.Z.
*Tripogon* Roem. & Schult. 1/20 Himalayas

LILIACEAE 17/3700
*Astelia* Banks & Soland. 6/25 Pacific & Reunion F
*Collospermum* Skotts. 5/5 N.Z., Fiji, Samoa F
*Dianella* Lam. 2/30 New Guinea F
*Smilacina* Desf. 4/25 C. Amer. F

ORCHIDACEAE 20,000/30,000
Approx. 500 genera, 20,000 species epiphytic, pantropical D

PANDANACEAE 4/700
*Pandanus* L. 4/600 Malaysia

PHILESIACEAE 2/10
*Luzuriaga* Ruiz & Pav. 2/3 N.Z., Chile F

RAPATEACEAE 6/80
*Epidryos* Maguire 3/3 S. Amer. D
*Stegolepis* Kl. ex Koern. 3/23 S. Amer. large D

ZINGIBERACEAE 14/700
*Brachychilum* (R. Br. ex Wall.) O. G. Petersen 2/2 Java F
*Hedychium* Koen. 12/50 Malaysia, India F

## DICOTYLEDONAE

AQUIFOLIACEAE 1/400
*Ilex* L. 1/400 Himalayas F

ARALIACEAE 73/700
*Pentapanax* Seem. 2/15 Java to Formosa F (hemi)
*Polyscias* J. R. & G. Forst 5/80 Malaya to N.Z. F (hemi)
*Schefflera* J. R. & G. Forst 60/200 pantropical F (hemi)
*Sciadophyllum* P. Br. 5/30 S. Amer. W.I. F (hemi)
*Tupidanthus* Hook. f. & Thoms. 1/1 Indomalaya F (hemi)

ASCLEPIADACEAE 135/2000
*Ceropegia* L. 3/160 New Guinea W
*Cynanchum* L. 2/150 neotropics W
*Dischidia* R. Br. 60/90 Indomalaya-Pacific W
*Dischidiopsis* Schlecht. 9/9 Phillipines. New Guinea W
*Heynella* Backer 1/1 Java W
*Hoya* R. Br. 60/200 Indomalaya-Pacific W

BALSAMINACEAE 5/550
*Impatiens* L. 5/500 Malaysia, neotropics

BEGONIACEAE 10/920
*Begonia* L. 10/900 Africa, Malaysia, S. Amer. F & D

BIGNONIACEAE 3/650
*Radermachera* Zoll. & Mor. Malaysia 1/40 W (?)
*Schlegelia* Miq. 2/18 neotropics F

CACTACEAE 133/2000
*Acanthorhipsalis* (Schum.) Br. & Rose 3/3 S. Amer. F
*Aporocactus* Lemaire 6/6 Mexico F
*Chiapasia* Br. & Rose 1/1 Mexico F
*Deamia* Br. & Rose 1/1 neotropics F
*Disocactus* Lindl. 2/2 C. Amer. F
*Eccremocactus* Br. & Rose 3/3 C. Amer. F
*Epiphyllanthus* Berg. 3/3 Brazil F
*Epiphyllum* Haworth 21/21 neotropics F
*Erythrorhipsalis* Berg. 1/1 Brazil F
*Hatiora* Br. & Rose 3/4 Brazil F
*Hylocereus* (Berg.) Br. & Rose 18/20 neotropics F
*Lepismium* Pfeiffer 1/1 Brazil F
*Mediocactus* Br. & Rose 2/2 Brazil F
*Nopalxochia* Br. & Rose 1/1 Mexico F
*Pfeiffera* Salm-Dyck 1/1 Argentina F
*Pseudorhipsalis* Br. & Rose 2/2 C. Amer. W.I. F
*Rhipsalis* Gaertn. 50/55 neotropics F
*Schlumbergera* Lem. 2/2 Brazil F
*Selenicereus* (Berg.) Br. & Rose 12/16 neotropics F
*Strophocactus* Br. & Rose 1/1 Brazil F
*Weberocereus* Br. & Rose 3/3 C. Amer. F
*Werckleocereus* Br. & Rose 2/2 C. Amer. F
*Wilmattia* Br. & Rose 1/1 C. Amer. F
*Wittia* Schum. 2/2 S. Amer. F
*Zygocactus* Schum. 1/1 Brazil F

CAMPANULACEAE 18/2000
*Centropogon* Presl. (incl. *Burmeistera*) 7/300 neotropics F
*Clermontia* Gaudich. 10/27 Hawaii F
*Cyanea* Gaudich. 1/60 Hawaii F

CELASTRACEAE 2/850
*Eunoymus* L. 2/175 Himalayas F (hemi)

CLUSIACEAE 92/1000
*Clusia* L. 85/145 Africa, Madagascar, neotropics F (hemi)
*Clusiella* Planch. & Triana 3/7 S. Amer. F (hemi)
*Havetiopsis* Planch. & Triana 1/5 S. Amer. F (hemi)
*Odematopus* Planch. & Triana 1/10 S. Amer. F (hemi)
*Quapoya* Aubl. 1/3 S. Amer. F (hemi)
*Renggeria* Meisn. 1/3 Brazil F (hemi)

COMPOSITAE 3/13,000
*Eupatorium* L. (s.l.) 1/1200 C. Amer. W
*Senicio* L. 2/2000 Mexico, N.Z. W

CRASSULACEAE 4/1500
*Echeveria* DC. 2/150 neotropics large D
*Sedum* L. 2/600 Himalayas D

CUNONIACEAE 3/250
*Ackama* A. Cunn. 1/3 N.Z. W (hemi)
*Weinmannia* L. 2/170 N.Z. W (hemi)

DULONGIACEAE 1/8
*Phyllonoma* Willd. ex Schult. 1/8 neotropics F (hemi)

ELAEOCARPACEAE 1/350
*Sericolea* Schlecht. 1/20 New Guinea F

ERICACEAE 483/1350
*Agapetes* D. Don ex G. Don 60/80 India, Malaysia F
*Anthopterus* Hook. 3/7 S. Amer. F
*Anthopteropsis* A. C. Smith 1/1 C. Amer. F
*Cavendishia* Lindl. 75/100 neotropics F
*Ceratostema* Juss. 15/18 S. Amer. F
*Costera* J. J. Sm. 8/8 Sumatra to Phillipines F
*Demosthenisia* A. C. Smith 2/9 S. Amer. F
*Dimorphanthera* F. Muell. 10/60 Malaysia F
*Diplycosia* Bl. 25/60 Indomalaya F
*Disterigma* Niedenzu ex Drude 15/35 S. Amer. F
*Empedoclesia* Sleum. 1/1 C. Amer. F
*Gaultheria* Kalm ex L. 8/200 India, Malaysia, S. Amer. F
*Gonocalyx* Planch. & Lind. ex A. C. Smith 1/3 neotropics F
*Lateropora* A. C. Smith 1/1 Panama F
*Lysiclesia* A. C. Smith 2/2 S. Amer. F
*Macleania* Hook. 25/45 S. Amer. F
*Orthaea* Kl. 10/15 S. Amer. F
*Plutarchia* A. C. Smith 6/12 S. Amer. F
*Psammisia* Kl. 20/50 neotropics F
*Rhododendron* L. 90/500 India, Malaysia W
*Rusbya* Britton 1/1 Bolivia F
*Satyria* Kl. 20/25 neotropics F
*Semiramisa* Kl. 7/7 Andes F
*Sphyrospermum* Poepp. & Endl. 16/16 neotropics F
*Symphysia* Presl 1/1 W.I., S. Amer. F
*Themistoclesia* Kl. 20/30 Andes F
*Thibaudia* Ruiz & Pav. 20/60 neotropics F
*Vaccinium* L. 15/350 pantropical F

GENTIANACEAE 1/900
*Leiphaimos* Cham. & Schlect. 1/40 S. Amer. D

GESNERIACEAE 549/2500
*Aeschynanthus* Jack 80/80 Indomalaya W
*Agalmyla* Bl. 15/15 Malaysia W
*Alloplectus* Mart. 25/65 neotropics F
*Alsobia* Hanst. 2/2 neotropics F
*Asteranthera* Hanst. 1/1 neotropics F
*Boea* Comm. ex Lam 1/25 New Guinea
*Capanea* Planch. 8/11 neotropics F
*Codonanthe* (Mart.) Hanst. 17/17 neotropics F
*Codonanthopsis* Mansf. 3/3 neotropics F
*Columnea* L. 70/70 neotropics F
*Cyrtandra* J. R. & G. Forst. 10/600 New Guinea F
*Dalbergaria* Tussac 65/65 neotropics F
*Dichrotrichum* Rienw. 4/4 Phillip to New Guinea W
*Drymonia* Mart. 100/110 neotropics F
*Fieldia* Cunn. 1/1 Australia F
*Heppiella* Regel 1/23 neotropics F
*Loxostigma* C. B. Cl. 3/4 India W
*Lysionotus* G. Don 2/2 Himalayas, Malaysia W
*Mitraria* Cav. 1/1 neotropics F
*Monopyle* Benth. 1/23 neotropics F
*Nematanthus* Schrader 26/26 neotropics F
*Neomortonia* Wiehler 1/1 neotropics F
*Paradrymonia* Hanst. 8/28 neotropics F
*Pentadenia* (Planch.) Hanst. 23/24 neotropics F
*Rufodorsia* Wiehler 4/4 neotropics F
*Sarmienta* Ruiz & Pav. 1/1 neotropics F
*Sinningia* Nees 3/60 neotropics F
*Streptocarpus* Lindl. 10/132 Africa D
*Trichantha* Hook. 70/70 neotropics F

GRISELINIACEAE 3/6
*Griselinia* Forst. f. 3/6 N.Z., Chile F (hemi)

LENTIBULARIACEAE 12/190
*Utricularia* L. 12/180 Africa, Madagascar, Australia, neotropics D

MARCGRAVIACEAE 94/130
*Caracasia* Szyszyl. 2/2 Venezuela F (hemi)
*Marcgravia* L. 50/55 neotropics F (hemi)
*Norantea* Aubl. 20/35 neotropics F (hemi)
*Souroubea* Aubl. 20/25 neotropics F (hemi)
*Ruyschia* Jacq. 2/10 neotropics (F) hemi

MELASTOMATACEAE 483/3000
*Adelobotrys* DC. 10/20 neotropics W
*Blakea* P. Br. 60/70 neotropics (F) hemi
*Calvoa* Hook. f. 4/20 Africa fr.?
*Catanthera* F. Muell. 5/5 Borneo, New Guinea F
*Clidemia* D. Don 6/145 neotropics F
*Creochiton* Bl. 4/6 Indomalaya F
*Hypenanthe* (Bl.) Bl. 4/4 New Guinea F
*Kendrickia* Hook. f. 1/1 India, Ceylon D
*Macrocentrum* Hook. f. 3/15 S. Amer. D
*Medinilla* Gaudich. 300/400 paleotropics F
*Medinillopsis* Cogn. 2/2 Malaysia F
*Memecylon* L. 1/300 New Guinea F
*Monolena* Triana 6/6 neotropics D
*Pachycentria* Bl. 7/8 India, Malaysia F
*Phainantha* Gleason 1/1 S. America W
*Pleiochiton* Naud. ex A. Gray 9/9 Brazil F
*Pogonanthera* Bl. 6/6 Malaysia F
*Preussiella* Gilg. 2/2 Africa F
*Salpinga* Mart. ex DC. 2/6 S. Amer. D
*Topobea* Aubl. 20/50 neotropics F (hemi)
*Triolena* Naud. 20/20 neotropics D
*Veprecella* Naud. 10/20 Madagascar fr.?

MORACEAE 521/1400
*Antiaropsis* K. Schum. 1/1 New Guinea
*Coussapoa* Aubl. 20/45 neotropics F (hemi)
*Ficus* L. 500/800 pantropical F (hemi)

MYRSINACEAE 28/1000
*Cybianthus* Mart. 5/40 S. Amer., W.I. F
*Embelia* Burm. 5/130 paleotropics F
*Grammadenia* Benth. 6/15 neotropics F (some hemi)
*Rapanea* Aubl. 12/200 pantropical F

MYRTACEAE 7/3000
*Mearnsia* Merr. 4/7 Phillipines to New Guinea, W
*Metrosideros* Banks ex Gaertn. 3/60 N.Z., W (hemi)

NEPENTHACEAE 6/70
*Nepenthes* L. 6/70 India to Pacific W

ONAGRACEAE 3/640
*Fuchsia* L. 3/100 neotropics F

PIPERACEAE 710/3100
*Peperomia* Ruiz & Pav. 700/1000 pantropics
*Piper* L. 10/2000 neotropics, Malaysia F

PITTOSPORACEAE 5/200
*Pittosporum* Banks ex Soland. 5/150 Malaysia, N.Z. F

POTALIACEAE 20/70
*Fagraea* Thunb. 20/35 Malaysia-Pacific F (hemi)

RANUNCULACEAE 1/1900
*Thalictrum* L. 1/150 Himalayas

ROSACEAE 3/2000
*Pyrus* L. 3/30 India-Malaysia F

RUBIACEAE 217/6000
*Amaracarpus* Bl. 3/60 New Guinea F
*Balmea* Martinez 1/1 Mexico W
*Coprosma* J. R. & G. Forst. 6/90 Malaysia, N.Z. Chile F
*Cosmibuena* Ruiz & Pav. 6/12 neotropics W
*Hillia* Jacq. 20/20 neotropics W
*Hydnophytum* Jack 75/80 Indomalaya to Pacific F
*Lecananthus* Jack 1/2 Malaysia F
*Lucinaea* DC. 15/25 Malaysia to New Caledonia F
*Malanea* Aubl. 2/20 neotropics F
*Manettia* Mutis ex L. 5/130 neotropics W
*Myrmecodia* Jack 40/45 Malaysia to Jiji F
*Myrmedoma* Becc. 2/2 New Guinea F
*Myrmephytum* Becc. 2/2 Phillipines, Celebes F
*Nertera* Banks & Soland. 6/12 Malaysia, Pacific F
*Ophiorrhiza* L. 5/150 New Guinea D
*Proscephaleium* Korth. 1/1 Java F
*Psychotria* L. 7/700 Malaysia, neotropics F
*Ravnia* Oerst. 4/4 C. America W
*Relbunium* Benth & Hook. f. 2/30 neotropics F
*Schradera* Vahl. 12/15 neotropics F
*Squamellaria* Becc. 2/2 Fiji F

SCROPHULARIACEAE 6/3000
*Gibsoniothamnus* L. O. Wms. 3/3 Panama
*Wightea* Wall. 3/3 Himalayas, Malaysia W

SOLANACEAE 33/2000
*Juanulloa* Ruiz & Pav. 12/12 neotropics F
*Lycianthes* Hassl. 2/200 Malaysia F
*Markea* L. C. Rich. 3/16 neotropics F
*Rahowardiana* D'Arcy 1/1 Panama F
*Solanum* L. 15/1700 Malaysia, neotropics F

URTICACEAE 41/550
*Elatostema* Gaudich. 10/200 Malaysia
*Pilea* Lindl. 20/400 neotropics Malaysia
*Pourouma* Aubl. 1/50 neotropics F
*Procris* Comm. ex Juss. 10/20 India, Malaysia F

VITACEAE 4/700
*Pterisanthes* Bl. 2/20 Malaysia F
*Tetrastigma* Planch. 2/90 Malaysia F

WINTERACEAE 1/120
*Drimys* J. R. & G. Forst. 1/70 New Guinea

## GEOGRAPHY

For this discussion three broad geographic areas are considered: tropical Africa; tropical Asia from India through southeast Asia and the Pacific area; and the neotropics. Madagascar, which has mixed geographic affinities in its epiphytic flora, is not included. The distribution of the genera and species of epiphytes in these regions is summarized in Table 2. The major features of the distribution are 1) the poverty of the epiphyte flora of Africa and the great diversity of epiphytes in the neotropics, with Asia intermediate in diversity, and 2) the much greater proportion of ferns and smaller proportion of non-orchidaceous monocotyledons in the paleotropics compared to the neotropics.

The poverty of the African epiphyte flora reflects a poverty of the entire wet tropical forest flora of Africa, and is apparently related to cycles of drier climate in Pleistocene times (Richards, 1973). More difficult to account for is the greater diversity of epiphytes in the neotropics than in Asia, regions which otherwise have wet tropical floras of comparable diversity. This difference in species diversity extends to biomass as well; there generally are

TABLE 2. GEOGRAPHICAL DISTRIBUTION OF EPIPHYTES (MADAGASCAR NOT INCLUDED)

| | | NEOTROPICS | ASIA & PACIFIC | AFRICA |
|---|---|---|---|---|
| Ferns & Gymnosperms | Genera | 35 | 73 | 21 |
| | Species | 840 | 1410 | 245 |
| Monocotyledons (less orchids) | Genera | 46 | 17 | 2 |
| | Species | 1640 | 200 | 5 |
| Dicotyledons | Genera | 124 | 94 | 12 |
| | Species | 2030 | 1580 | 120 |
| Subtotal | Genera | 205 | 168 | 35 |
| | Species | 4510 | 3190 | 370 |
| Orchid species | | 11,000 | 7,000 | 2,000 |
| Total species | | 15,510 | 10,190 | 2,370 |

fewer epiphytic plants in the tropical Asian vegetation, (personal communication from Kiat Tan). This may in part reflect a difference in habitat; the millions of acres of middle elevation cloud forest in the Andes where most of the neotropical epiphytes are found do not have as extensive a counterpart in Asia. Another factor is the historical accident of the distributions of certain families. The Bromeliaceae, Cactaceae, Marcgraviaceae, Cyclanthaceae, and Gesneriaceae subfamily Gesnerioideae are confined to the neotropics where they contribute a large number of species to the epiphyte flora.

To some extent paleotropical ferns may be filling niches occupied by monocotyledons in the neotropics, but in addition there seem to be a large number of epiphyte niches which are unexploited in the paleotropics. A case in point is that of large water- and litter-impounding rosettes. One of the most characteristic growth forms of new world epiphytes is a rosette of large leaves perched on the limb of a tree; this is found in numerous genera and species of Bromeliaceae, about 80 species of *Anthurium* (Araceae), *Philodendron* (Araceae), *Cochliostema* (Commelinaceae), *Yucca* (Agavaceae), *Asplenium* (Aspleniaceae) and less perfectly in *Elaphoglossum* (Aspidiaceae) and *Paradrymonia* (Gesneriaceae). In the old world this growth form is found only in *Asplenium* and in a few Pacific island species of *Astelia* (Liliaceae) and *Collospermum* (Liliaceae).

The differing proportion of ferns, non-orchid monocotyledons, and dicotyledons between the neotropical and paleotropical epiphyte floras is puzzling. As already indicated the absence of certain monocotyledonous families from Asia and the substitution of ferns in their characteristic niches are elements of an explanation, but it appears that in addition the constellation of circumstances necessary for an extensive radiation of paleotropical monocotyledons into epiphytic habitats has simply not come about as it has in the neotropics.

## DISPERSAL IN EPIPHYTES

The evolution of dispersal mechanisms in epiphytes has been molded by the necessity of the diaspores to reach the highly specialized habitats suitable for germination on the surfaces of trees. The dispersal of epiphyte seeds has been discussed by Schimper (1888) and briefly by Ridley (1930) and van der Pijl (1969). A summary of results based on the list of genera in Table 1 is as follows.

Of the 850 genera of vascular epiphytes, 605 have dust-seeds or spores which lack appendages, are well under 1 mm in length, and are dispersed

by wind and/or rain splash. Rauh et al. (1975) have studied the morphology of dust seeds and found that they characteristically exhibit a highly sculptured epidermis composed of dead air-filled cells which are considered to aid in their flotation as atmospheric dust. Diaspores of this type are found in the ferns and orchids, as well as in some Melastomataceae, Begoniaceae, Lentibulariaceae, and Rapateaceae.

A second category includes seeds larger than in the first group which are aided in wind dispersal by epidermal appendages such as wings or hairs. As in dust seeds, in most of these the epidermis is composed of dead air-filled cells. Some examples of evolutionary convergence in morphology of seeds of this type are illustrated in Figures 1-8. Winged or plumed seeds are found in 37 genera and 1190 species of epiphytes, and are characteristic of many Bromeliaceae, Asclepiadaceae, Gesneriaceae, and Rubiaceae.

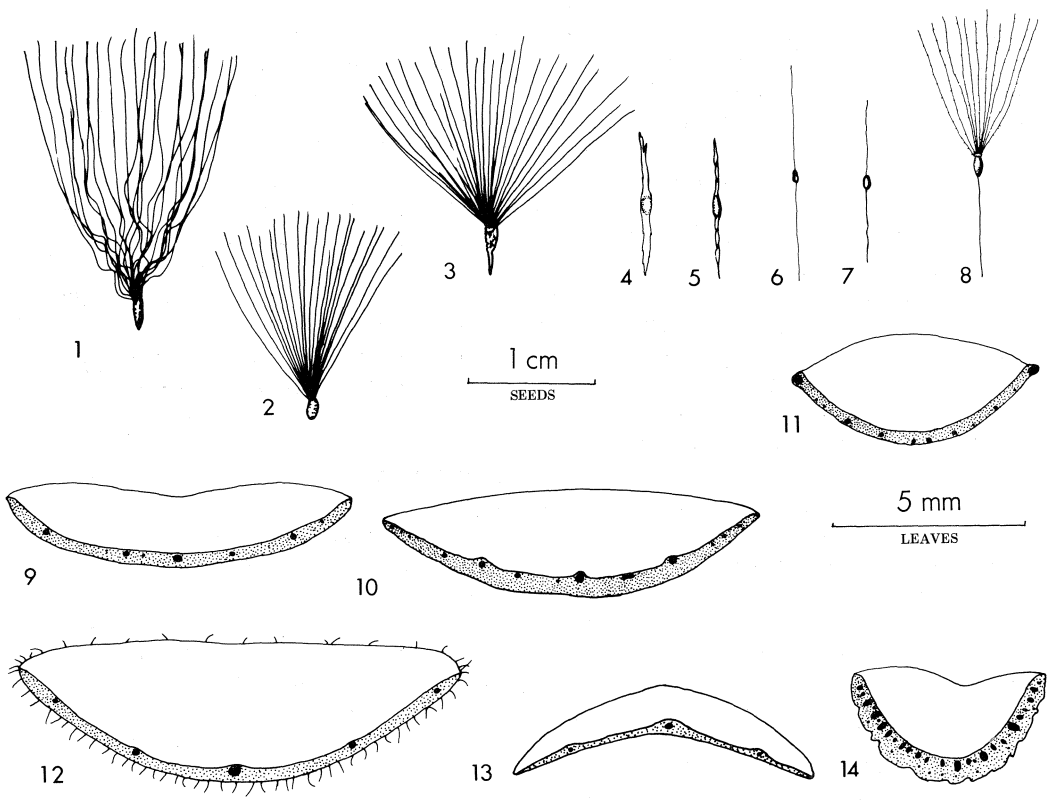


Plate 1

Figures 1-14. 1-8. Seeds of epiphytes, showing convergent evolution of external morphology. 1, *Catopsis floribunda* (Brongn.) L. B. Smith (Bromeliaceae); 2, *Dischidia gaudichaudii* Decaisne (Asclepiadaceae); 3, *Hillia parasitica* Jacq. (Rubiaceae); 4, *Cosmibuena macrocarpa* (Benth.) Klotzsch (Rubiaceae); 5, *Nepenthes spectabilis* Danser (Nepenthaceae); 6, *Aeschynanthus pulcher* G. Don (Gesneriaceae); 7, *Rhododendron vaccinioides* Hooker f. (Ericaceae); 8, *Aeschynanthus longicaulis* Wall. (Gesneriaceae); 9-14. Transections of epiphyte leaves, showing hypodermis. Stippling indicates chlorophyll-containing tissues. 9, *Peperomia* sp. (Piperaceae); 10, *Medinilla ledifolia* Hort. (Melastomataceae); 11, *Pleurothallis microphylla* A. Rich. & Gal. (Orchidaceae); 12, *Codonanthe carnosa* (Gardner) Hanst. (Gesneriaceae); 13, *Psychotria guadeloupensis* (DC.) Howard (Rubiaceae); 14, *Acanthostachys strobilacea* (Schult. f.) Klotzsch (Bromeliaceae).

Fleshy fruits, including dehiscent fruits with animal dispersed seeds such as are found in *Pittosporum*, *Hedychium*, and *Drymonia*, are found in 191 genera and about 4400 species of epiphytes. Most of these fleshy fruits contain numerous minute seeds with highly sculptured epidermis which when removed from the fruit are very similar to the dust-seeds of capsular fruited epiphytes.

A few genera exhibit other modes of dispersal, such as wind dispersal of vegetative gemmae in *Psilotum* and *Remusatia*, and occasional external dispersal of adhesive fruits in *Peperomia*.

The predominance of wind dispersal among epiphytes (84% of the species) is apparent, and is in contrast to terrestrial plants of wet tropical forests where wind dispersal is much less common. The dispersability of wind-borne diaspores is increased by their release from high above the ground. Thus for wind-dispersed plants of diminutive stature the evolution of an epiphytic habit greatly enhances dispersability; this may constitute a selection pressure favoring evolution of epiphytism which acts more strongly on wind-dispersed than animal-dispersed species. In this context it should be noted that the literature on epiphytism usually mentions only interception of more incident light as the advantage of the epiphytic habit. Of additional importance to epiphytes, are the conspicuous placement of flowers (e.g. in hummingbird pollinated species) and of fruits (dispersed by wind, birds, or bats). Another factor of unknown significance is the evasion of terrestrial predators by epiphytes.

Schimper (1888) emphasized that a proper type of fruit and seed is the most critical pre-adaptation in the evolution of epiphytism. This assumption may be debatable, but it can at least partly explain the lack of epiphytes in some large families which are ecologically and morphologically very diverse, e.g. Leguminosae, Euphorbiaceae.

## Germination and Establishment

A notable feature of epiphyte seeds is their small size; the majority of species have seeds less than 1 mm long and nearly all have seeds less than 2 mm. While small seed size is significant in dispersal, it is equally critical to successful germination and establishment.

One aspect of this is the well-known inverse relationship of seed number and seed size — plants making minute seeds can produce a great many of them as opposed to only a few big seeds with the same expenditure of energy (Harper et al., 1970). In epiphytes which require a very specific seedling habitat, successful reproduction may best be insured by saturating an area with a rain of small seeds of which a few will land in a suitable spot. This is especially relevant in species in which establishment of the seedling depends on association with a mycorrhiza, as in various ferns and orchids, Burmanniaceae, and possibly Ericaceae, *Pittosporum*, and others.

A second feature of seed size is its relation to the microrelief of the bark of the host tree. Even relatively smooth bark has small fissures where a slight accumulation of dust or humus could serve as a germination site for minute seeds but not big ones. The probability of landing in a suitable germination site is greater for small epiphyte seeds.

An additional significance of seed size in epiphytes involves the rate of imbibition of sufficient water for germination. Small seeds have a larger surface-volume ratio than big seeds, and consequently given an equal permeability will complete their imbibition faster and with less water. This may

be critical in a habitat which is normally dry and where availability of water is intermittent and often brief. In a few species with relatively large seeds, (e.g. *Anthurium*, *Pittosporum*), the seed is immersed in a thick jacket of mucilage which may serve to increase imbibition rate (Harper & Benton, 1966).

The importance of small seed size is illuminated in comparing related terrestrial and epiphytic species. For example, in *Anthurium* the true epiphytes have seeds about 2 mm long compared to 4-8 mm in terrestrially germinating species; in the tribe Monstereae (Araceae) the true epiphytes (*Stenospermation* spp.) have much smaller seeds than the hemi-epiphytic species; the epiphytic Cactaceae are characterized by smaller seeds than the terrestrial species, and so on.

An additional feature of epiphyte seeds is that most lack dormancy; if they are placed in a suitable habitat they will germinate readily. Indeed, vivipary is common in Araceae, Gesneriaceae, Cactaceae, and other fleshy-fruited epiphytes where already-germinating seeds are often found in ripe fruits. The absence of dormancy reflects in part the likelihood that the requirements of dispersal (e.g. air-filled epidermal cells in dust-seeds) are incompatible with the elaboration of a hard seed coat characteristic of most seeds exhibiting dormancy. Also, most epiphytes occur in regions where there is sufficient available moisture for germination in any month of the year, so that dormancy to evade a dry season is unnecessary.

In some epiphytes the germinating seed immediately elaborates a succulent structure; this may be the cotyledons (*Rhipsalis*, *Tillandsia*) the hypocotyl (*Hydnophytum*, *Souroubea*, *Ficus*, *Epiphyllum*), the protocorm (Orchidaceae), or the root (*Anthurium*, *Hedychium*). The function of these succulent structures is perhaps the storage of water allowing the young plant to survive intermittent drought until it is established. On the other hand, some epiphytes which are quite succulent as adults have seedlings that are tender and delicate (*Peperomia*, *Gesneriaceae*). The biology of seedlings is an aspect of epiphytes much in need of investigation.

## Attachment to the Host Tree

More than 99% of the genera of vascular epiphytes have species with adventitious roots, i.e. roots arising from the stem rather than from ramifications of the primary root system. The adhesion of these to the bark of the host tree is the usual method of attachment. These roots have been shown to be ageotropic and negatively heliotropic in some epiphytic orchids and aroids (Went, 1895).

This feature may have a bearing on the systematic composition of the epiphytic plant association, and in particular on the predominance of ferns and monocotyledons among epiphytes both in numbers of species and of individuals. Monocotyledons and ferns, whether epiphytic or terrestrial, normally produce adventitious roots since their primary root system is limited in growth by its lack of a vascular cambium. Dicotyledons and gymnosperms, in which the primary root system can increase in thickness by secondary growth, normally do not produce adventitious roots. In this regard the terrestrial ferns and monocotyledons share an important pre-adaptation for the evolution of an epiphytic habit.

The nearly universal presence of adventitious roots in epiphytes confers on them the ability for clonal reproduction by fragmentation of the plant; each branch has its own roots and may persist independently. In this way

a species with a creeping stem may colonize an entire tree after successful establishment of a single seedling.

A second feature of epiphytes relating to their attachment to the host is the common occurrence of pendulous shoots. They are especially frequent in Gesneriaceae, Cactaceae, and Ericaceae, and are found at least occasionally in nearly all other families with epiphytic species. A plant with shoots hanging down on both sides of a horizontal branch cannot be blown or knocked off the branch as easily as an erect plant on top of the branch. The most extreme manifestation of this is the bromeliad *Tillandsia usneoides* which usually lacks roots and is attached to trees only by hanging over branches.

No matter how well an epiphyte is attached to its host, if the branch on which it sits falls to the ground it loses the advantages of its habitat. Shedding of branches is a normal occurrence in healthy trees, and even large limbs may be dropped in diseased or injured individuals. This provides selection pressure for rapid maturation among epiphytes, which implies the elaboration of reproductive structures by small individuals. Conversely, small, rapidly-maturing plants can grow epiphytically on twigs or even leaves, habitats unavailable to larger epiphytes. Plants which at maturity are less than 10 cm tall are found in many species of ferns and orchids (especially Pleurothallidinae), *Peperomia*, (Piperaceae) *Macrocentrum*, (Melastomataceae), and others. Extremes of this trend are found in *Platystele jungermannioides* Schlecht. (Orchidaceae) in which a flowering plant is only 1 cm tall, and *Monogramma* (Vittariaceae) with mature plants about 3 mm by 2 cm.

## Aspects of Water Relations

The epiphytic habitat is subject to frequent, rapid, and extreme fluctuations in the availability of water. The surface of a tree may be flooded during a rain and yet be dry half an hour later. To accommodate to this situation most epiphytes exhibit devices for the trapping and storage of water and the diminuition of its loss during dry periods.

It may be noted that most vascular epiphytes live in very wet places; they are typically most abundant in tropical montane forests characterized by daily precipitation throughout the year. In such forests the trees are covered by a thick mantle of bryophytes which by their sponge-like character moderate the severity of fluctuations in available water. Even in this environment many epiphytes show xeromorphic adaptations, though the most extreme xeromorphic features are found in epiphytes inhabiting regions with a pronounced dry season.

Any accumulation of humus in the tree, in addition to being a source of mineral nutrients will serve as a water reservoir. Basket-like structures which are formed from negatively geotropic roots and serve to accumulate litter are found in various epiphytes, most elaborately in the Orchidaceae (e.g. *Cyrtopodium*) and *Anthurium*. Dimorphic leaves with one form serving as a humus-catching bracket are also common; the most familiar example is *Platycerium*, but this form also occurs in *Drynaria*, *Dischidia*, *Hoya*, *Polypodium*, *Monstera*, *Marcgravia*, *Rhaphidophora*, *Teratophyllum*, and others. Examples of rosulate species which impound water and litter in tightly overlapping leaf bases have been mentioned already.

The storage of water in a succulent tissue is a nearly universal trait in vascular epiphytes. Water may be stored in fleshy roots (e.g. *Hedychium*, *Medinella*, *Pachycentria*, *Campylocentrum*), in stems (Orchidaceae, Cacta-

ceae, Gesneriaceae, *Hydnophytum, Macleania, Peperomia*), in petioles (*Philodendron*) and peduncles (*Begonia, Monolena*). Perhaps the most common form of water storage however is a uniseriate or multiseriate hypodermis below the adaxial surface of the leaf. This may be so considerable as to constitute 80% of the thickness of the leaf; some extreme forms are illustrated in Figures 9-14. An aqueous hypodermis is found in nearly all epiphytic Gesneriaceae, Ericaceae, Marcgraviaceae, Clusiaceae, Araliaceae, and *Peperomia*, in orchids, most epiphytic Melastomataceae, Rubiaceae, *Pittosporum, Cochliostema, Metrosideros, Fagraea, Begonia, Griselinia, Platycerium, Elaphoglossum, Hoya, Coussapoa, Ficus, Pourouma, Weinmannia*, and nearly all epiphytic bromeliads (Metcalfe & Chalk, 1950, and personal observation). Metcalfe & Chalk (1950) note that a hypodermis is found only in the epiphytic species of *Psychotria*.

Schimper (1888:37) and Haberlandt (1914: 397-403) have shown that when detached leaves of epiphytes are left in a dry room over a period of days the hypodermis shrinks while the photosynthetic tissues remain turgid, demonstrating the function of the hypodermis as a water reserve for the mesophyll. This interpretation has been reiterated by Gessner (1956) whereas Keating (1975) has proposed that the hypodermis acts as a lens focusing light on the mesophyll, an interesting hypothesis but probably not significant.

In addition to its role as a water storage tissue, the hypodermis may be significant in the heat economy of epiphytes which exhibit crassulacean acid metabolism. Coutinho (1965, 1969) has demonstrated the occurrence of crassulacean acid metabolism in a number of epiphytic bromeliads and orchids. In these species the stomata are closed during the day and open at night when the plant fixes $CO_2$ into organic acids. The significance of this metabolic pathway to the plants is that they can carry on photosynthesis during the day without water loss by transpiration through open stomata, using as a carbon source the $CO_2$ incorporated into organic acids during the night. A possible significance of the hypodermis in this regard is in the heat economy of the leaf. In mesic terrestrial plants, cooling of an illuminated leaf is effected primarily by transpiration, and secondarily by convection and radiation. In an epiphyte with its stomata closed during the day and with limited water resources in general, transpiration may not be a feasible method of cooling. In such a case a thick hypodermis could act as a shield of high heat capacity to dampen oscillations of temperature as the leaf is periodically exposed to sunflecks or shade.

## SUMMARY

About 28,000 species of vascular plants in 65 families normally grow epiphytically; in other words, somewhat more than 10% of the known species of vascular plants are epiphytes. In their systematic composition the epiphytes are more diverse in the neotropics than in the paleotropics. Non-orchidaceous monocotyledons comprise a much greater proportion of the epiphytes flora in the neotropics, whereas ferns are more significant in the paleotropics.

Most species of epiphytes (80%) have minute, unappendaged, wind-dispersed diaspores; the remainder have fleshy fruits (16%) or appendaged wind-dispersed seeds (4%). Regardless of mechanism of dispersal, epiphytes have small seeds (generally less than 1 mm long) with a highly sculptured epidermis and which lack dormancy. Other common features of epiphytes are animal pollination, rapid maturation, adventitious roots, pendulous

shoots, simple leaves (more than 90%), and succulence, especially in the form of a multiseriate hypodermis below the adaxial surface of the leaf. While none of the features is unique to epiphytes, in the aggregate they serve to characterize this interesting group of plants.

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